Impact of dust addition on the microbial food web under present and future conditions of pH and temperature

Julie Dinasquet[1,2*], Estelle Bigeard[3], Frédéric Gazeau[4], Farooq Azam[1], Cécile Guieu[4], Emilio Marañón[5], Céline Ridame[6], France Van Wambeke[7], Ingrid Obernosterer[2] and Anne-Claire Baudoux[3]

[1] Marine Biology Research Division, Scripps Institution of Oceanography, UCSD, USA

[2] Sorbonne Université, CNRS, Laboratoire d'Océanographie Microbienne, LOMIC, France

[3] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR 7144 Adaptation et Diversité en Milieu Marin, France

[4] Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, 06230 Villefranche-sur-Mer, France

[5] Department of Ecology and Animal Biology, Universidade de Vigo, Spain

[6] CNRS-INSU/IRD/MNHN/UPMC, LOCEAN: Laboratoire d'Océanographie et du Climat: Expérimentation et Approches Numériques, UMR 7159

[7] Aix-Marseille Université, CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography, UM110, France

[*]Corresponding: jdinasquet@ucsd.edu, present address: Center for Aerosol Impact on Chemistry of the Environment (CAICE), Scripps Institution of Oceanography, UCSD, USA

Keywords: bacteria, microeukaryotes, virus, community composition, top-down

Abstract

In the oligotrophic waters of the Mediterranean Sea, during the stratification period, the microbial loop relies on pulsed inputs of nutrients through atmospheric deposition of aerosols from both natural (*e.g.* Saharan dust), anthropogenic or mixed origins. While the influence of dust deposition on microbial processes and community composition is still not fully constrained, the extent to which future environmental conditions will affect dust inputs and the microbial response is not known. The impact of atmospheric wet dust deposition was studied both under present and future environmental conditions (+3°C warming and acidification of -0.3 pH units), through experiments in 300 L climate reactors. Three Saharan dust addition experiments were performed with surface seawater collected from the Tyrrhenian Sea, Ionian Sea and Algerian basin in the Western Mediterranean Sea during the PEACETIME cruise in May-June 2017. Top-down controls on bacteria, viral processes, and community, as well as microbial community structure (16S and 18S rDNA amplicon sequencing) were followed over the 3-4 days experiments. Different microbial and viral responses to dust were observed rapidly after addition and were most of the time more pronounced when combined to future environmental conditions. The dust input of nutrients and trace metals changed the microbial ecosystem from bottom-up limited to a top-down controlled bacterial community, likely from grazing and induced lysogeny. The relative abundance of mixotrophic microeukaryotes and phototrophic prokaryotes also increased. Overall, these results suggest that the effect of dust deposition on the microbial loop is dependent on the initial microbial assemblage and metabolic state of the tested water, and that predicted warming, and acidification will intensify these responses, affecting food web processes and biogeochemical cycles.

1. Introduction

Input of essential nutrients and trace metals through aerosol deposition is crucial to the ocean surface water biogeochemistry and productivity (at the global scale: *e.g.,* Mahowald et al., 2017; in the Mediterranean Sea: *e.g.,* Guieu and Ridame, 2020) with episodic fertilization events driving microbial processes in oligotrophic regions such as the Pacific Ocean, the Southern Ocean and the Mediterranean Sea.

The summer Mediterranean food web is characterized by low primary production (PP) and heterotrophic prokaryotic production (more classically abbreviated as BP for bacterial production) constrained by nutrient availability. Low BP further limits dissolved organic matter (DOM) utilization and export, resulting in DOM accumulation. Therefore, inputs of bioavailable nutrients through deposition of atmospheric particles are essential to the Mediterranean Sea microbial ecosystem. Indeed, these nutrient pulses have been shown to support microbial processes but the extent to which the microbial food web is affected might be dependent on the degree of oligotrophy of the water (Marín-Beltrán et al., 2019; Marañon et al., 2010).

In the Mediterranean Sea, dust deposition may stimulates PP and N_2 fixation (Guieu et al., 2014; Ridame et al., 2011, 2021) but also BP, bacterial respiration, virus production, grazing activities, and can alter the composition of the microbial community (*e.g.,* Pulido-Villena et al., 2014; Tsiola et al., 2017; Guo et al., 2016; Pitta et al., 2017; Marín-Beltrán et al., 2019). Overall, in such oligotrophic system, dust deposition appears to predominantly promote heterotrophic activity which will increase respiration rates and CO_2 release.

Anthropogenic CO_2 emissions are projected to induce an increase in seawater temperature and an accumulation of CO_2 in the ocean, leading to its acidification and an alteration of ocean carbonate chemistry (IPCC, 2014). In response to ocean warming and increased stratification,

low nutrient low chlorophyll (LNLC) regions such as the Mediterranean Sea, are projected to expand in the future (Durrieu de Madron et al., 2011). Moreover, dust deposition is also expected to increase due to desertification (Moulin and Chiapello, 2006). For these reasons, in the future ocean, the microbial food web might become even more dependent on atmospheric deposition of nutrients. Expected increased temperature and acidification might have complex effects on the microbial loop by modifying microbial and viral and community (*e.g.,* Highfield et al., 2017; Krause et al., 2012; Hu et al., 2021; Allen et al., 2020; Malits et al., 2021). While increasing temperature in combination with nutrient input might enhance heterotrophic bacterial growth (Degerman et al., 2012; Morán et al., 2020) more than PP (Marañón et al., 2018), future environmental conditions could push even further this microbial community towards heterotrophy. But so far, the role of dust on the microbial food web in future climate scenarios is unknown.

Here, we studied the response of Mediterranean microbial and viral communities (*i.e.,* viral strategies, microbial growth and controls, as well as community composition) to simulated wet Saharan dust deposition during onboard minicosm experiments conducted in three different basins of the Western and Central Mediterranean Sea under present and future projected conditions of temperature and pH. To our knowledge, this is the first study assessing the effect of atmospheric deposition on the microbial food web under future environmental conditions.

2. Material & Method

2.1 Experimental set-up

During the 'ProcEss studies at the Air-sEa Interface after dust deposition in the MEditerranean sea' project cruise (PEACETIME), onboard the R/V "Pourquoi Pas ?" in May/June 2017, three experiments were conducted in 300 L climate reactors (minicosms) filled with surface seawater collected at three different stations (Table 1), in the Tyrrhenian Sea (TYR), Ionian Sea (ION) and in the Algerian basin (FAST). The experimental set-up is described in details in Gazeau et al. (2021a). Briefly, the experiments were conducted for 3 days (TYR and ION) and 4 days (FAST) in trace metal free conditions, under light, temperature and pH-controlled conditions following ambient or future projected conditions of temperature and pH. For each experiment, the biogeochemical evolution of the water, after dust deposition, under present and future environmental conditions was followed in three duplicate treatments: i) CONTROL (C1, C2) with no dust addition and under present pH and temperature conditions, ii) DUST (D1, D2) with dust addition under present environmental conditions and iii) GREENHOUSE (G1, G2) with dust addition under projected temperature and pH for 2100 (IPCC, 2014; ca. +3 °C and -0.3 pH units). Water was acidified by addition of CO_2 saturated 0.2 µm filtered seawater and slowly warmed overnight (Gazeau et al, 2021a). The same dust analog was used as during the DUNE 2009 experiments as described in Desboeufs et al. (2014) and the same dust wet flux of 10 g m^{-2} was simulated (as described in Gazeau et al 2021a). Briefly, the dust was derived from the <20 µm fraction of soil collected in Southern Tunisia (a major source for material transported and deposited in the Northwestern Mediterranean) with most particles (99%) smaller than 0.1 µm (Desboeufs et al., 2014). The collected material underwent an artificial chemical aging process by addition of nitric and sulfuric acid (HNO_3 and H_2SO_4,

107 respectively) to mimic cloud processes during atmospheric transport of aerosol with
108 anthropogenic acid gases (Guieu et al., 2010, and references therein). To mimic a realistic wet
109 flux event for the Mediterranean of 10 g m^{-2}, 3.6 g of this analog dust were quickly diluted in 2 L
110 ultrahigh-purity, and sprayed at the surface of the dust amended treatments (D1, D2 and G1, G2;
111 Gazeau et al., 2021a). Such deposition event represents a high but realistic scenario, as several
112 studies reported even higher short wet deposition events in this area of the Mediterranean Sea
113 (Ternon et al., 2010; Bonnet and Guieu, 2006; Loÿe-Pilot and Martin, 1996), suggesting that wet
114 deposition is the main pathway of dust input in the Western Medirranean Sea.

115 Samples for all parameters (except described below) were taken at t-12h (while filling the
116 tanks), t0 (just before dust addition), t1h, t6h, t12h, t24h, t48h, t72h and t96h (after dust addition,
117 and t96h only for FAST).

118 *2.2. Growth rates, mortality, and top down controls*

119 BP was estimated at all sampling points from rates of ^{3}H-Leucine incorporation
120 (Kirchman et al., 1985; Smith and Azam, 1992) as described in Gazeau et al. (2021b). Briefly,
121 triplicate 1.5 mL samples and one blank were incubated in the dark for 1-2 h after addition of 20
122 nM of a mix of cold and ^{3}H-leucine in two temperature-controlled incubators maintained
123 respectively at ambient temperature for C1, C2, D1 and D2 and at ambient temperature +3 °C for
124 G1 and G2. Heterotrophic prokaryotes (HB)and heterotrohic nanoflagellates (HNF) abundances
125 were measured by flow cytometry as described in Gazeau et al. (2021a). Briefly, samples (4.5
126 mL) were fixed with glutaraldehyde grade I (1% final concentration) and stored at -80°C until
127 analysis. Counts were performed on a FACSCanto II flow cytometer (Becton Dickinson©). Cells
128 were stained with SYBR Green I at 0.025% (vol / vol) final concentration (Gasol & DelGiorgio
129 2000, Christaki et al 2011). Bacterial biomass specific growth rates (BBGR) were estimated

following Kirchman (2002), BP/Bacterial Biomass, assuming a carbon to cell ration of 20 fg C cell^{-1} (Lee and Fuhrman, 1987). Mortality was estimated as the difference between HB present between two successive sampling points and those produced during that time.

2.3. Viral abundance, production and life strategy

Virus abundances were determined on glutaraldehyde fixed samples (0.5% final concentration, Grade II, Sigma Aldrich, St Louis, MO, USA) stored at -80 °C until analysis. Flow cytometry analysis was performed as described by Brussaard (2004). Briefly, samples were thawed at 37 °C, diluted in 0.2 µm filtered autoclaved TE buffer (10:1 Tris-EDTA, pH 8) and stained with SYBR-Green I (0.5×10^{-4} of the commercial stock, Life Technologies, Saint-Aubin, France) for 10 min at 80 °C. Virus particles were discriminated based on their green fluorescence and SSC during 1 min analyses (Fig. S1). All cytogram analyses were performed with the Flowing Software freeware (Turku Center of Biotechnology, Finland).

Viral production and bacterial losses due to phages were assessed by the virus reduction approach (Weinbauer et al., 2010) at t0 and t24 h in all six minicosms. Briefly, 3 L of seawater were-filtered through 1.2-µm-pore-size polycarbonate filter (Whatman©), and HB (filtrate) were concentrated by ultrafiltration (0.22 µm pore size, Vivaflow 200© polyethersulfone, PES) down to a volume of 50 mL. Virus-free water was obtained by filtering 1 L of seawater through a 30 kDa pore-size cartridge (Vivaflow 200©, PES). Six mixtures of HB concentrate (2 mL) diluted in virus-free water (23 mL) were prepared and distributed into 50 mL Falcon tubes. Three of the tubes were incubated as controls, while the other three were inoculated with mitomycin C (Sigma-Aldrich, 1 µg mL^{-1} final concentration) as inducing agent of the lytic cycle in lysogenic bacteria. All tubes were incubated in darkness in two temperature-controlled incubators maintained respectively at ambient

152 temperature for C1, C2, D1 and D2 and at ambient temperature +3 °C for G1 and G2. Samples for
153 HB and viral abundances were collected every 6 h for a total incubation period of 18 h.
154 The estimation of virus-mediated mortality of HB was performed according to Weinbauer et al.
155 (2002) and Winter et al. (2004). Briefly, increase in virus abundance in the control tubes represents
156 lytic viral production (VPL), and an increase in treatments with mitomycin C represents total viral
157 production (VPT), *i.e.,* lytic plus lysogenic, viral production. The difference between VPT and
158 VPL represents lysogenic production (VPLG). The frequency of lytically infected cells (FLIC)
159 and the frequency of lysogenic cells (FLC) were calculated as:
160 $FLIC = 100 \times VPL / BS \times HB_i$ (1)
161 $FLC = 100 \times VPLG / BS \times HB_i$ (2)
162 where HB_i is the initial HB abundance in the viral production experiment and BS is a theoretical
163 burst size of 20 viruses per infected cell (averaged BS in marine oligotrophic waters, Parada et al.,
164 2006).
165
166 *2.4 DNA sampling, sequencing and sequence analysis*

167 To study the temporal dynamics of the microbial diversity, water samples (3 L) were
168 collected in acid-washed containers from each minicosm at t0, t24h, and at the end of the
169 experiments (t72h at TYR and ION and t96h at FAST). Samples were filtered onto 0.2 µm PES
170 filters (Sterivex©) and stored at -80 °C until DNA extraction. Nucleic acids were extracted from
171 the filters using a phenol-chloroform method and DNA was then purified using filter columns from
172 NucleoSpin® PlantII kit (Macherey-Nagel©) following a modified protocol. DNA extracts were
173 quantified and normalized at 5 ng μL^{-1} and used as templates for PCR amplification of the V4
174 region of the 18S rRNA (~380 bp) using the primers TAReuk454FWD1 and TAReukREV3

(Stoeck et al., 2010) and the V4-V5 region of the 16S rRNA (~411 bp) using the primers 515F-Y (5'-GTGYCAGCMGCCGCGGTAA) and 926R-R (5'-CCGYCAATTYMTTTRAGTTT) (Parada et al., 2016). Following polymerase chain reactions, DNA amplicons were purified, quantified and sent to Genotoul (https://www.genotoul.fr/, Toulouse, France) for high throughput sequencing using paired-end 2x250bp Illumina MiSeq. Note that although we used universal primer, Archaea were mostly not detected and the prokaryotic heterotrophic communities corresponded essentially to Eubacteria, therefore the taxonomic description referred to the general term 'bacterial communities'

All reads were processed using the Quantitative Insight Into Microbial Ecology 2 pipeline (QIIME2 v2020.2, Bolyen et al., 2019). Reads were truncated 350bp based on sequencing quality, denoised, merged and chimera-checked using DADA2 (Callahan et al., 2016). A total of 714 and 3070 amplicon sequence variants (ASVs) were obtained for 16S and 18S respectively. Taxonomy assignments were made against the database SILVA 132 (Quast et al., 2013) for 16S and PR2 (Guillou et al., 2013) for 18S. All sequences associated with this study have been deposited under the BioProject ID: PRJNA693966.

2.5 Statistics

Alpha and beta-diversity indices for community composition were estimated after randomized subsampling to 26000 reads for 16S rDNA and 19000 reads for 18S rDNA. Analysis were run in QIIME 2 and in Primer v.6 software package (Clarke and Warwick, 2001). Differences between the samples richness and diversity were assessed using Kruskal-Wallis pairwise test. Beta diversity was run on Bray Curtis dissimilarity. Differences between samples' beta diversity were tested using PERMANOVA (Permutational Multivariate Analysis of Variance) with pairwise test and 999 permutations. The sequences contributing most to the

198 dissimilarity between clusters were identified using SIMPER (similarity percentage). A linear
199 mixed model was performed using the R software (R Core Team, 2020) using the 'nlme'
200 package (Pinheiro et al., 2014) to test if the amended treatments differed from the controls at
201 t24h and t72h or t96h.

3. Results

3.1. Microbial growth, mortality and top-down controls

Nutrients inputs were observed with dust addition (Fig. S2) and in response the autotrophic and heterotrophic microbial abundances increased, as well as BP (Fig. S3), as described in more details in Gazeau et al (2021a, b). Already 24h following dust addition, significant increases in heterotrophic bacterial biomass specific growth rates (BBGR, $p \leq 0.016$ at t24 h) were observed in all experiments with dust under D and G as seen in Fig. 1 (showing data normalized to C) and Fig. S4. The highest growth rates were observed already 24 h after dust seeding (up to 2.9 d^{-1} in G2 at FAST, Table S1, Fig.S4). At 24h, in both D and G, heterotrophic bacterial mortality rates were higher than in C (Fig. 1), especially at TYR in D (up 0.5 d^{-1}) and in G at ION (up to 0.6 d^{-1}) and FAST (up to 0.7 d^{-1}, Table S1). Over the course of the three experiments, the slope of the linear regression between log bacterial biomass and log bacterial production was below 0.4 in the three treatments suggesting a weak bottom up control (Fig. 2A; Ducklow, 1992). The slope decreased in D and G relative to C. Overall, the top-down index, as described by Morán et al. (2017), was higher in G (0.92) relative to C and D (0.80). The relationship between log transformed HNF and log bacterial abundance (Fig. 3B), plotted according to the model in Gasol (1994), showed that HNF were below the MRA (Mean realized HNF abundance) in all treatments, suggesting a top-down control of HNF abundance. HNF and bacteria were weakly coupled in all treatments. The relationship between total viruses and bacterial abundance was weaker in D and G relative to C (Fig. S5).

3.2. Viral dynamics and processes

224 The initial abundance and production of virus-like particles (VLP) was higher in the
225 western stations (Table 1). Viral strategy (lysogenic vs. lytic replication) was also different
226 between stations, with a higher frequency of lysogenic cells (FLC) at TYR and ION (23 and
227 19%, respectively, Table 1) and a higher frequency of lytically infected cells (FLIC) at FAST
228 (43%, Table 1).

229 During TYR and ION experiments, the relative contribution of VLP populations was similar
230 and stable over time with Low DNA viruses representing over 80% of the community (Figs. 3
231 and S5). The Low DNA VLP abundance was however slightly higher in D and G relative to C
232 after 24 h at TYR and significantly higher at ION after 48h ($p = 0.037$; Fig. 4). In contrast to the
233 other two stations, at FAST, Giruses (giant viruses, characterized by high DNA fluorescence and
234 high SSC) were also present and increased in all treatments but especially in G where they made
235 up to 9% of the viral community at the end of the experiment (Figs. 3 and 4). The abundance of
236 high DNA viruses at FAST also increased independent of treatments and accounted for 16 – 18%
237 of the community at the end of the experiment (Figs. 3 and 4).

238 The sampling strategy for production and life strategies of HB viruses allowed to
239 discriminate independently the effect of i) greenhouse conditions (sampling at T0 before dust
240 addition), ii) dust addition (sampling at t24h) and the combined effects of dust addition and
241 greenhouse. Lytic viral production (VPL) increased significantly at T0 in G at TYR and ION
242 compared to C ($p \leq 0.036$). The addition of dust induced higher VPL in D at TYR (normalized to
243 C, Fig.1). No significant impact of dust on VPL was observed in G compared to D after 24h for
244 any of the experiments. Changes in viral infection strategy were observed with G conditions at
245 T0 where FLC decreased relative to the non-G treatments at TYR and ION, and especially at
246 FAST (Fig. 1, $p = 0.047$). FLIC increased slightly in G at TYR and ION already at T0. Dust

addition had no detectable significant effect on this parameter for any experiments. Looking at the relative share between lytic and lysogenic infection, dust addition favored lytic infection at TYR (no lysogenic bacteria were observed after 24h) but the contribution of both infection strategies remained unchanged compared to C at ION and FAST. Greenhouse conditions also favored replication through lytic cycle already at T0 for all three experiments and this trend was not impacted by dust addition.

3.3. Microbial community composition

Microbial community structure, bacteria and micro-eukaryotes from 16S rDNA and 18S rDNA sequencing respectively, responded to dust addition in all three experiments relative to C (Figs. 5 and 6). After quality controls, reads were assigned to 714 and 1443 ASVs for 16S and 18S respectively.

3.3.1. Bacterial community composition

The initial community composition (t-12h) was significantly different at the three stations (PERMANOVA; $p = 0.001$, Fig. S6a, S7). Rapid and significant changes in the bacterial community composition were observed already 24 h after dust addition (Fig. 4). Despite the initial different communities, the three stations appeared to converge towards a closer community composition in response to dust addition (Fig. S7). At TYR, communities in D and G significantly changed 24 h after dust addition (PERMANOVA; $p = 0.001$). This cluster presented no significant differences between treatments (D and G) or time (24 and 72 h). The differences between C and D/G were attributed to a relative increase of ASVs related to different *Alteromonas* sp., OM60 and *Pseudophaeobacter* sp. and *Erythrobacter* sp.; contribution of ASVs related to SAR11 and Verrucomicrobia and *Synechococcus* decreased (Table S2a). At

ION, the bacterial community composition significantly changed 24 h after dust addition (PERMANOVA; $p = 0.001$) and was significantly different between D and G (PERMANOVA; $p = 0.032$). As observed at TYR, no further change occurred between 24 h and the end of the experiment (72 h; Fig. 5). The difference between the controls and dust amended minicosms were assigned to an increase of ASVs related to different *Alteromonas* sp., *Erythrobacter* sp., *Dokdonia* sp. and OM60, and a decrease of ASVs related to SAR11, *Synechococcus*, Verrucomicrobia, Rhodospirillales and some Flavobacteria (Table S2b). Several ASVs related to *Alteromonas* sp., *Synechococcus* sp. and *Erythrobacter* sp. were further enriched in G compared D while *Dokdonia* sp. was mainly present in D. At FAST, the bacterial community after 24 h only significantly changed in G (PERMANOVA; $p = 0.011$; Fig. 5). However, after 96 h, the community in D and G were similar and appeared to transition back to the initial state at 96 h (PERMANOVA; $p = 0.077$). The higher relative abundance in *Erythrobacter* sp., *Synechoccocus* sp., different ASVs related to *Alteromonas* sp. and Flavobacteria appeared to contribute mainly to the difference between C and D/G (Table S2) while ASVs related to SAR11, Verrucomicrobia, *Celeribacter* sp. *Thalassobius* sp. and Rhodospirillales were mainly present in C (Table S2c).

3.3.2 Nano- and micro-eukaryotes community composition

The diversity of initial community was large (Fig. S7) and significantly different at the three stations (PERMANOVA; $p = 0.001$; Fig. S6b). At TYR, the nano- and micro-eukaryotes community responded rapidly (24 h) to dust addition (PERMANOVA; $p = 0.003$). This initial high diversity disappeared after 72 h, with similar communities in all minicosms (Fig. S7). They were significantly different from initial and t24h communities ($p = 0.002$ and 0.03 respectively; Fig 6) in D/G. The variations at t24h were attributed to changes in the dinoflagellate

communities in particular to an increase in ASVs related to *Heterocapsa rotundata*, Gymnodiniales and Gonyaulacales as well as to an increase in Chlorophyta (Table S3a). At ION, no significant changes were observed between C and D/G after 24 h. However, after 72 h, the communities were significantly different in D ($p = 0.018$) and G ($p = 0.05$) compared to the communities at t24h in these treatments (Table S3b). In D, diversity was significantly higher at t72h compared to t24h and to C at the same sampling time ($p = 0.036$). In contrast, diversity in G at t72h was lower than at t24h and lower to the one observed in C at the same sampling time ($p = 0.066$; Fig S8). These differences were mainly attributed to changes in ASVs related to dinoflagellates and to the increase at t72h of *Emiliana huxleyi* and Chlorophyta in D and G, respectively (Table S3b). At FAST, significant differences were observed between the controls and initial communities compared to the dust amended (D and G) treatments at t24h ($p = 0.036$). No major differences were observed between D/G at t24h and t96h ($p = 0.06$). The differences were mainly attributed to changes in dinoflagellates ASVs and to an increase in Acantharea and *Emiliana huxleyi* in D and G treatments at t96h (Table S3c).

4. Discussion

Pulsed inputs of essential nutrients and trace metals through aerosol deposition are crucial to surface microbial communities in LNLC regions such as the Mediterranean Sea (reviewed in Guieu and Ridame, 2020). Here we assessed the impact of dust deposition on the late spring microbial loop under present and future environmental conditions on the surface water of three different Mediterranean basins (Tyrrhenian, TYR; Ionian, ION; and Algerian, FAST). The initial conditions at the three sampled stations for the onboard experiments are described in more details in Gazeau et al. (2021a). Briefly, very low levels of dissolved inorganic nutrients were measured at all three stations, highlighting the oligotrophic status of the waters. This is typical of the stratified conditions generally observed in the Mediterranean Sea in late spring/early summer (*e.g.,* Bosc et al., 2004; D'Ortenzio et al., 2005). Despite similar total chl. *a* concentrations at the three stations (Gazeau et al., 2021a), PP was higher at FAST (Table 1, Gazeau et al., 2021b; Marañón et al., 2021). The initial microbial communities differed substantially between the three stations as shown by pigments (Gazeau et al., 2021a), 18S and 16S rDNA sequencing (this study). DOC concentrations were slightly higher at TYR where PP was the lowest (Gazeau et al., 2021b). HB, HNF abundances (Gazeau et al., 2021a), as well as viral abundance and production increased following the east to west gradient of the initial water conditions.

The dust addition induced similar nitrate + nitrite (NO_x) and dissolved inorganic phosphate (DIP) release during all three experiments. Rapid changes were observed on plankton stocks (autotroph and heterotroph abundances and chl.*a*, Gazeau et al., 2021a) and metabolisms (BP and PP, Gazeau et al., 2021b), suggesting that the impact of dust deposition is constrained by the initial composition and metabolic state of the investigated community. While no direct effect of warming and acidification was observed on the amount of nutrient released from dust, Gazeau et

al. (2021a, b) showed that biological processes were generally enhanced by these conditions and suggested that deposition may weaken the biological pump in future climate conditions. Here we are further investigating how dust addition in present and future conditions affected, on a short-term scale (≤ 4 days), the microbial trophic interactions and community composition.

4.1. Trophic interactions after dust addition under present and future conditions

Parallel nutrient enrichment incubations conducted in darkness showed that *in situ* heterotrophic bacterioplankton communities (initial conditions of the present experiments), were N, P co-limited at TYR, mainly P limited at ION and N limited at FAST (Van Wambeke et al., 2021). However, after incubation, the HB appeared to be weakly bottom up controlled (Ducklow, 1992) especially in D and G (Fig 2a) after dust addition. Such top-down control on the bacterioplankton has been previously observed in the Mediterranean Sea, where the bacterioplankton community lives in a dynamic equilibrium between grazing pressure and nutrients limitation, as reviewed by Siokou-Frangou et al., 2010. Moreover, potential increase under future conditions as suggested by the higher top-down index in G (G = 0.92 vs. C/D= 0.80, Morán et al., 2017) should be further assessed.

Bacterial mortality increased relative to controls in D and G at TYR, and only in G at ION and FAST. The weak coupling between bacteria and viruses, as well as the increased virus production and relative abundance of lytic cells (see below), only explained a small fraction of the estimated bacterial mortality (max. 17%), suggesting an additional grazing pressure on bacteria. Nanoflagellates bacterivory can account for up to 87% of bacterial production in the Mediterranean Sea, however rates can be variable in space and time (Siokou-Frangou et al, 2010). Here, HNF abundances increased in D at TYR and at all stations in G (Gazeau et al., 2021a), which could explain the increased bacterial mortality. Increased grazing rate by HNF on

352 bacteria with dust addition has been previously reported in the Eastern Mediterranean Sea
353 (Tsiola et al., 2017). While our results suggest a strong grazing pressure on bacteria, no direct
354 coupling between HNF and bacteria were observed, probably because HNF appeared to be top-
355 down controlled themselves (Gasol, 1994, Fig 3b), potentially by the increasing populations of
356 mixotrophic dinoflagellates and/or Giruses (see below), this suggest intensification of trophic
357 cascades in the microbial loop with nutrient input. It is also possible that HB were grazed by
358 mixotrophic nanoflagellates or by larger protozoans, or that the HNF abundance was
359 underestimated by flow cytometry. Towards the end of the experiment bacterial growth and
360 mortality may also have been linked to DIP depletion at TYR and ION.

361 Considering the seasonal impact of grazing and viral mortality in the Mediterranean Sea,
362 where higher grazing pressure and lysogeny were observed in the stratified nutrient-limited
363 waters in summer (Sánchez et al., 2020), it will be important to further study the seasonal impact
364 of dust deposition on trophic interactions and indirect cascading impact on microbial dynamics
365 and community composition.

366

367 *4.2. Viral processes and community during dust enrichment in present and future conditions*

368 Viruses represent pivotal components of the marine food web, influencing genome evolution,
369 community dynamics, and ecosystem biogeochemistry (Suttle, 2007). The impacts of marine
370 viruses differ depending on whether they establish lytic or lysogenic infections (Zimmerman et
371 al. 2019, Howard-Varona et al. 2017). Understanding how viral infection processes are
372 influenced by changes in environmental conditions, is thus crucial to better constrain microbial
373 mortality and cascading effects on marine ecosystems. Aerosol deposition was already identified

374 as a factor that stimulates virus production and viral induced mortality of bacteria in the
375 Mediterranean Sea (Pulido-Villena et al., 2014; Tsiola et al., 2017) and direct deposition of
376 airborne viruses and viruses attached to dust particles may also affect microbial food webs
377 (Sharoni et al., 2015; Rahav et al., 2020). However, the impact of future environmental
378 conditions remains more controversial (Larsen et al., 2008; Brussaard et al., 2013; Maat et al.,
379 2014; Vaqué et al., 2019; Malits et al., 2021). The combined effect of aerosol deposition and
380 future conditions of temperature and pH on the viral compartment has, to our knowledge, never
381 been investigated.
382 The rapid changes in viral production and lifestyle observed in all three experiments support the
383 idea that the viral component is sensitive to the environmental variability even on short (hourly)-
384 time scales. The dynamics in viral activities was however impacted differently depending on the
385 treatments and the experiments. Viral production increased in D and G at TYR and only in G at
386 ION and FAST. Regarding the G treatments, increase in viral production was detected before
387 dust addition for all three experiments and remained mostly unchanged for the remaining of the
388 incubation. This suggests that water warming, and acidification were responsible for most
389 changes in viral activities while dusts had no detectable impact in such conditions regardless of
390 the studied station. Based on our results, the most likely explanation for observed changes in
391 viral production is an activation of a lysogenic to lytic switch. The factors that result in prophage
392 induction are still not well constrained, but nutrients pulses and elevated temperatures have been
393 identified as potential stressors (Danovaro et al., 2011 and references therein). Consistent with
394 the observation of N, P co-limited bacterial community at TYR, it is likely that nutrients released
395 from dust upon deposition to surface water activate the productive cycle of temperate viruses at
396 this station. Such mechanism was also speculated during another dust addition study (Pulido-

Villena et al., 2014). Under future conditions (G), the low proportion of lysogens was associated to higher frequency of lytically infected cells relative to C and D at TYR and ION. These trends probably reflect an indirect effect of enhanced bacterial growth with increased temperature not only on prophage induction (Danovaro et al., 2011; Vaqué et al., 2019; Mojica and Brussaard, 2014) but also on the kinetics of lytic infections. Intriguingly, the enhanced viral production did not translate into marked changes in viral abundance. The abundance of Low DNA virus population, which typically comprises virus of bacteria, actually decreased between t0 and t48h pointing to possible viral decay, potentially related to an adsorption onto dust particles (Weinbauer et al., 2009;Yamada et al., 2020) and the potential export of viral particle to deeper water layers (Van Wambeke et al. 2021). While recurrent patterns emerged from this study, the amplitude of viral responses varied between the experiments. At TYR, where heterotrophic metabolism was higher, the dust addition induced higher viral production relative to controls than at the two other sites, which suggests that viral processes, as other microbial processes, are dependent on the initial metabolic status of the water.

Overall, no marked changes were observed for viral communities and abundances after dust addition, both under present and future conditions relative to controls, except at FAST where the abundance of Girus population increased significantly in G from t24h until the end of the experiment. Giruses typically comprise large double stranded DNA viruses that infect nanoeukaryotes including photosynthetic (microalgae) and heterotrophic (HNF, amoeba, choanoflagellate) organisms (Brussaard and Martinez, 2008; Needham et al., 2019; Fischer et al., 2010; Martínez et al., 2014). The presence of Giruses at FAST in this treatment might be explained by the increase in nano-eukaryote abundances at t72h and their decline after 96 h of incubation (Gazeau et al., 2021a). The coccolithophore *Emiliania huxleyi* appears as one of the

potential host candidates for these Giruses. The abundance of *E. huxleyi* increased in D and G at this station and this phytoplankter is known to be infected by such giant viruses (Jacquet et al., 2002; Schroeder et al., 2002; Pagarete et al., 2011). It is not clear from our results whether increased Girus abundance is due to the greenhouse effect only (as discussed above for viruses of HB) or the combination of dust addition and greenhouse effects. While temperature warming was shown to accelerate viral production in several virus – phytoplankton systems (Mojica and Brussaard 2014, Demory et al. 2017), a temperature-induced resistance to viral infection was specifically observed in *E. huxleyi* (Kendrick et al., 2014). Previous experiments have also reported a negative impact of acidification on *E. huxleyi* virus dynamics (Larsen et al., 2008). By contrast, nutrient release following dust seeding could indirectly stimulate *E. huxleyi* virus production (Bratbak et al., 1993) or induced switching between non-lethal temperate to lethal lytic stage (Knowles et al.,2020) under future conditions. Targeted analyses are of course required to identify the viral populations selected in G and the outcomes of their infection. Nonetheless, this is the first time, to our knowledge, that dust deposition and enhanced temperature and acidification have been shown to induce the proliferation of Giruses. The impact of dust deposition under future environmental conditions on the viral infections processes could have significant consequences for microbial evolution, food web processes, biogeochemical cycles, and carbon sequestration.

4.3 Microbial community dynamic after dust addition under present and future conditions

While changes in bacterial community composition during various type of dust addition experiments have shown only minor transient responses (*e.g.,* Marañon et al., 2010; Hill et al., 2010; Laghdass et al., 2011; Pulido-Villena et al., 2014; Marín-Beltrán et al., 2019), here

443 microbial community structure showed quick, significant and sustained changes in response to
444 dust addition in all three experiments. Similar to other parameters observed during these
445 experiments (discussed above and in Gazeau et al., 2021a, b), the degree of response in terms of
446 community composition was specific to the tested waters.

447 At TYR, where primary production was low, only transient changes after 24 h of incubation
448 were observed, before the micro-eukaryotes community converged back close to initial
449 conditions. In contrast, the bacterial community significantly and rapidly changed after 24 h and
450 remained different after 72 h. At FAST, where the addition of dust appeared to promote
451 autotrophic processes, the micro-eukaryotes community responded quickly 24 h after dust
452 addition, while minor and delayed changes, probably related to the lower growth rates compared
453 to the other tested waters, were observed in the bacterial community. At ION both eukaryotes
454 and bacterial community responded to dust addition. The delayed response of micro-eukaryotes
455 after 72 h compared to the quick bacterial response at 24 h suggests that HB were better at
456 competing for nutrient inputs at this station and that autotrophic processes may be responding to
457 bacterial nutrient regeneration after a lag phase, further suggesting the tight coupling between
458 heterotrophic bacteria and phytoplankton at this station. The combined effect of decreased pH
459 and elevated temperature on marine microbes is not yet well understood (reviewed in O'Brien et
460 al., 2016). The absence of significant community changes at TYR and FAST while changes were
461 observed at ION, suggests that the response might be dependent on other environmental factors,
462 which need to be further studied.

463 Dust addition likely favors certain group of micro-organisms, suggesting a quicker response
464 of fast growing/copiotrophic groups as well as the increase of specialized functional groups (Guo
465 et al., 2016; Westrich et al., 2016; Maki et al., 2016). Potential toxicity effects of metals and

biological particles released from dust/aerosols on certain micro-organisms have also been reported (Paytan et al., 2009; Rahav et al., 2020). Here, the micro-eukaryotic community was dominated by a diverse group of dinoflagellates which were responsible for the main variations between treatments at all stations. The overwhelming abundance of dinoflagellates sequences over other micro-eukaryotes could be biased by the large genomes and multiple ribosomal gene copies per genome found in dinoflagellates (Zhu et al., 2005) or due to their preferential amplification. However, the dominance of dinoflagellates in surface water at this time of the year in the Mediterranean Sea is not uncommon (García-Gómez et al., 2020) and was also observed in surface waters of the three sampled stations by Imaging Flow Cytobot (Marañón et al., 2021). While pigment data suggest an increase of haptophytes and pelagophytes in D (Gazeau et al., 2021a), the sequencing data only show the presence of *Emiliana huxleyi* as responsible for some of the community changes after dust addition at ION and FAST. These pigments could also indicate the presence of dinoflagellates through tertiary endosymbiosis, in particular *Karlodinium* sp. (Yoon et al., 2002; Zapata et al., 2012), which is an important mixotrophic dinoflagellate (Calbet et al., 2011) observed in D and G at ION and FAST. The variations in dinoflagellate groups might have important trophic impacts due to their diverse mixotrophic states (Stoecker et al., 2017) and the effect of dust addition on mixotrophic interactions should be further studied to better understand the cascading impact of dust on food webs and the biological pump.

Positive to toxic impacts on cyanobacteria have been reported from atmospheric deposition experiments (*e.g.,* Paytan et al., 2009; Zhou et al., 2021, Rahav et al., 2020). Here, *Synechococcus* appeared to be inhibited at TYR while it was enhanced at ION and FAST, especially under future conditions (this study, Gazeau et al., 2021a). The same ASVs appeared to

be inhibited at TYR and ION while promoted at FAST and a different ASVs increased at ION. *Synechococcus* has recently been shown to be stimulated by wet aerosol addition in P-limited conditions but inhibited in N-limited conditions, in the South China Sea (Zhou et al., 2021). It was also shown to be repressed by dust addition in nutrient limited tropical Atlantic (Marañon et al., 2010). This suggests that different *Synechococcus* ecotypes (Sohm et al., 2016) might respond differently to dust addition depending on the initial biogeochemical conditions of the water.

In the three experiments, the main bacterial ASVs responsible for the differences between the control and treatments were closely related to different *Alteromonas* strains. *Alteromonas* are ubiquitous in marine environment and can respond rapidly to nutrient pulses (López-Pérez and Rodriguez-Valera, 2014). Some *Alteromonas* are capable to grow on a wide range of carbon compounds (Pedler et al., 2014). They can produce iron binding ligands (Hogle et al., 2016) to rapidly assimilate Fe released from dust. Thus, they could have significant consequences for the marine carbon and Fe cycles during dust deposition events. Other copiotrophic γ-Proteobacteria, such as *Vibrio,* have been observed to bloom after dust deposition in the Atlantic Ocean (Westrich et al., 2016). Guo et al. (2016) using RNA sequencing, also show that γ-Proteobacteria quickly outcompete α-Proteobacteria (mainly SAR11 and Rhodobacterales) that were initially more active. Here, while SAR11 relative abundance decreased in all experiments after 24h, other α-Proteobacteria related to the aerobic anoxygenic phototroph (AAP) *Erythrobacter* sp., increased in response to dust, in particular under future conditions. Other AAP, such as OM60, also responded to dust addition in our experiment and in the Eastern Mediterranean Sea (Guo et al., 2016). Moreover, bacteriochlorophyll a, a light harvesting pigment present in AAP, was generally higher in dust addition treatments especially under future conditions compared to

512 controls (Fig. S9). Fast growing AAP might quickly outcompete other HB by supplementing
513 their growth with light derived energy (*e.g.,* Koblížek, 2015). They have also been shown to be
514 stimulated by higher temperature (Sato-Takabe et al., 2019). AAP response to dust and future
515 conditions could have a significant role in marine biogeochemical cycles.

516 **5. Conclusion**

517 The microbial food web response to dust addition was dependent on the initial state of the
518 microbial community in the tested waters. A different response in trophic interactions and
519 community composition of the microbial food web, to the wet dust addition, was observed at
520 each station. Generally greater changes were observed in future conditions. Pulsed input of
521 nutrients and trace metals changed the microbial ecosystem from bottom-up limited to a top-
522 down controlled bacterial community, likely from grazing and induced lysogeny. The
523 composition of mixotrophic microeukaryotes and phototrophic prokaryotes was also altered.

524 Overall, the impact of such simulated pulsed nutrient deposition will depend on the initial
525 biogeochemical conditions of the ecosystem, with likely possible large impact on microbial
526 trophic interactions, in particular viral processes, and community structure. All effects might be
527 generally enhanced in future climate scenarios. The impact of dust deposition on metabolic
528 processes and consequences for the carbon and nitrogen cycles and the biological pump based on
529 these minicosm experiments are further discussed in Gazeau et al. (2021b) and Ridame et al.
530 (2021), and the *in situ* effect of a wet dust deposition event is explored in Van Wambeke et al.
531 (2021), in this special issue.

532 **6. Data availability**

All data and metadata will be made available at the French INSU/CNRS LEFE CYBER database (scientific coordinator: Herve Claustre; data manager, webmaster: Catherine Schmechtig; INSU/CNRS LEFE CYBER, 2020). All sequences associated with this study have been deposited under the BioProject ID: PRJNA693966.

7. Author contributions

FG and CG designed the experiment. All authors participated in sampling or sample processes. JD analyzed the data and wrote the paper with contributions from all authors.

8. Competing interests

The authors declare that they have no conflict of interest.

9. Financial support

This study is a contribution to the PEACETIME project (http://peacetime-project.org, https://doi.org/10.17600/17000300), a joint initiative of the MERMEX and ChArMEx components supported by CNRS-INSU, IFREMER, CEA, and Météo-France as part of the programme MISTRALS coordinated by INSU. PEACETIME was endorsed as a process study by GEOTRACES and SOLAS. Part of this research was funded by the ANR CALYPSO attributed to ACB (ANR-15-CE01-0009). EM was supported by the Spanish Ministry of Science, Innovation and Universities through grant PGC2018-094553B-I00. JD was funded by a Marie Curie Actions-International Outgoing Fellowship (PIOF-GA-2013-629378).

10. Acknowledgements

554 We gratefully acknowledge the onboard support from the captain and crew of the RV Pourquoi
555 Pas? and of our chief scientists C. Guieu and K. Desboeuf. We also thank K. Djaoudi, J. Uitz, C.
556 Dimier, P. Catala, B. Marie and M. Perez-Lorenzo with their assistance in sampling and analysis
557 of pigments, microbial abundance, DOC concentration and primary production. We thank the
558 two referees for their inputs.
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Tables and Figures

Table1: Initial conditions (t-12h) at the three stations sampled for the dust addition experiments. Other parameters are presented in more details in Gazeau et al. (2020; 2021)

Variables	TYR	ION	FAST
Location	Tyrrhenian Basin	Ionian Basin	Algerian Basin
Coordinates	39.34N, 12.60E	35.49N, 19.78E	37.95N,2.90E
Temperatures (°C)	20.6	21.2	21.5
DOC (µM)[2]	72.2	70.2	69.6
Chlorophyll *a* (µg L^{-1})[1]	0.063	0.066	0.072
BP (ng C L^{-1} h^{-1})[2]	11.6	15.1	34.6
Bacterial abundance (x10^5 cells mL^{-1})[1]	4.79	2.14	6.15
BBGR (d^{-1})	0.03	0.08	0.07
Viral abundance (x 10^6 VLP mL^{-1})	3.01	1.44	2.79
% Lysogenic bacteria FLC	22.7	19.4	7.8
% Lytic bacteria FLIC	17.5	37.2	42.7
Viral production (x 10^4 VLP mL^{-1} h^{-1})	2.05	1.36	7.99
HNF abundance (cells mL^{-1})[1]	110	53	126
Diatoms (cells L^{-1})[1]	340	900	1460
Dinoflagellates (cells L^{-1})[1]	2770	3000	3410
Ciliates (cells L^{-1})[1]	270	380	770

DOC: dissolved organic carbon, BP: heterotrophic prokaryotic production, BBGR: bacterial biomass specific growth rates, HNF: Heterotrophic nanoflagellates

[1]Results presented in Gazeau et al. 2021a

[2]Results presented in Gazeau et al. 2021b

Figure legends:

Figure 1. Bacterial and viral parameters in the three experiments (TYR, ION and FAST) in each minicosm (D1, D2, G1 and G2). The values are normalized to the controls: the data are presented as the difference between the treatments and the mean value of the duplicate controls. The first row represents the bacterial biomass specific growth rates (BBGR) and relative mortality rates at t24h after dust addition. The second raw represents the relative viral productions at t24h and at T0 for the G treatments. The last raw represents the viral strategies: the percentages of lytic (FLIC) or lysogenic (FLC) cells at t24h and at T0 for the G treatments.

Figure 2. (A) Log-log linear regression between bacterial biomass and bacterial production, dotted lines represent linear regressions for each treatment. (B) Relationships between log HNF abundance and log bacterial prey abundance. Solid black and dotted black lines corresponds to the Mean Realized HNF Abundance (MRA) and theoretical Maximum Attainable HNF Abundance line (MAA) respectively. The samples are grouped per treatments.

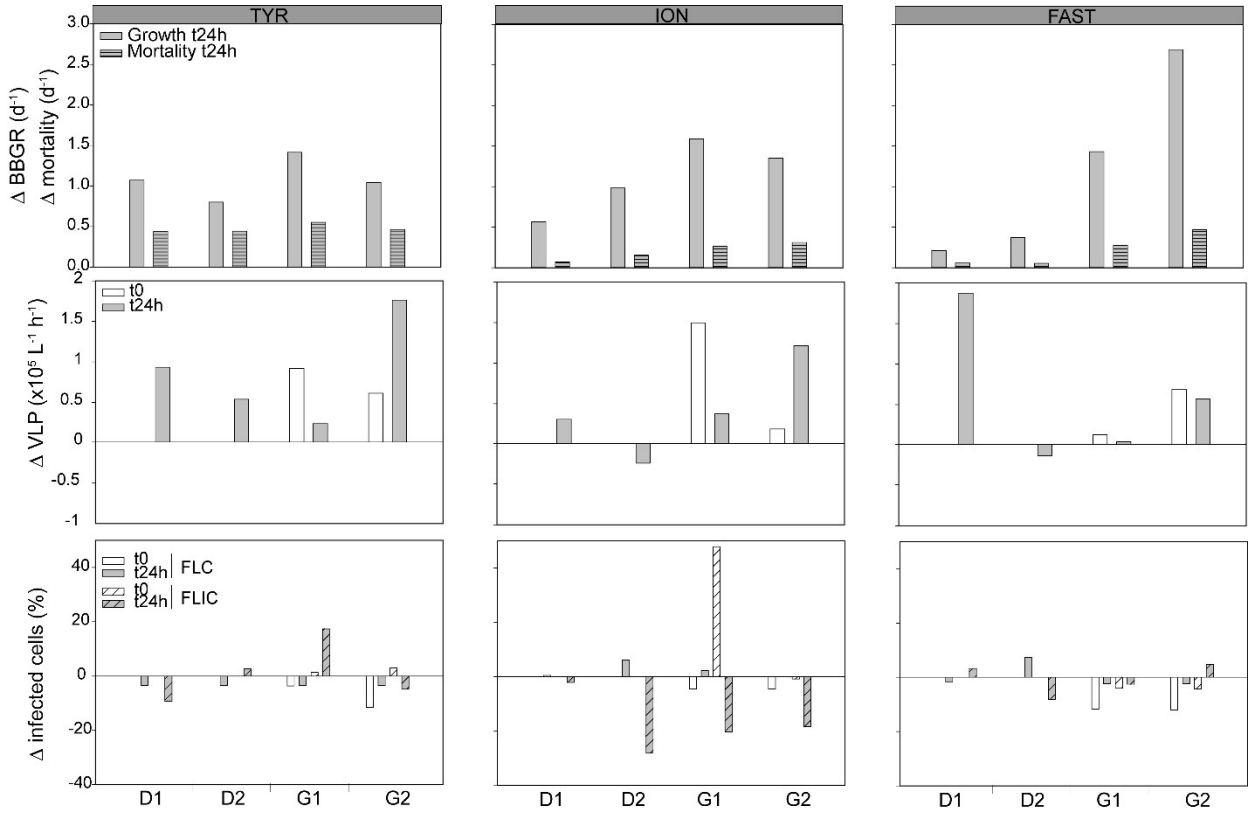
Figure 3. Relative abundance of viral populations at the initial (*in situ*: at t-12h before dust addition) and final time points in all minicosms (C1, C2, D1, D2, G1 and G2) during the three experiments (TYR, ION and FAST).

Figure 4. Evolution of Virus like particles abundances (VLP) of three different viral populations over the course of the three experiments (TYR, ION and FAST). The first row represents low DNA viruses or phages, the second row represents high DNA viruses, and the third row represents giant viruses (Giruses).

Figure 5. nMDS plot of bacterial community composition over the course of the three experiments based on Bray-Curtis dissimilarities of 16S rDNA sequences. Samples clustering at different level of similarity are circled together. All circles represent clusters which are significantly different from each other ($p < 0.05$) based on a PERMANOVA test.

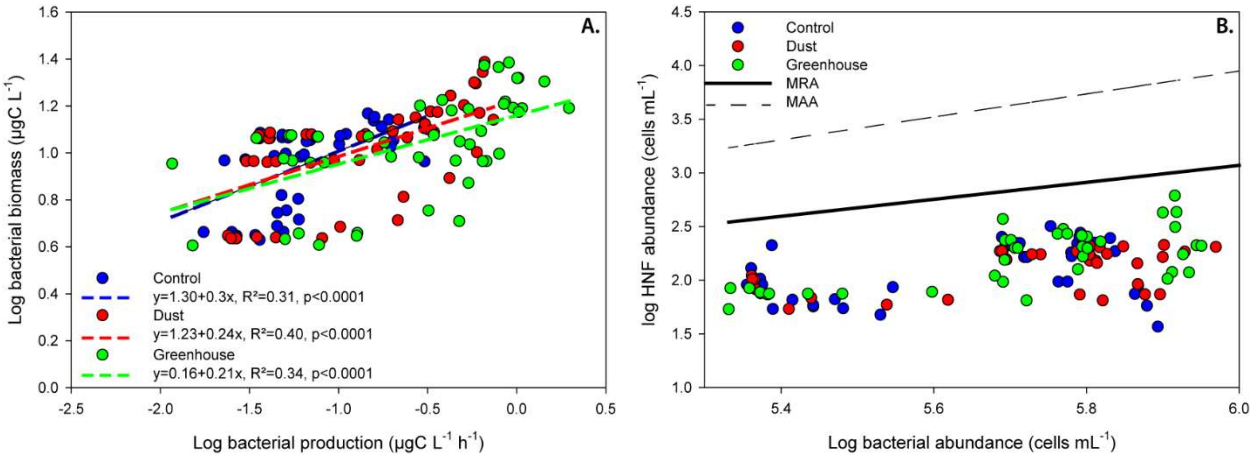
Figure 6. nMDS plot of micro-eukaryotes community composition over the course of the three experiments based on Bray-Curtis dissimilarities of 18S rDNA sequences. Samples clustering at different level of similarity are circled together. All circles represent clusters which are significantly different ($p < 0.05$) from each other based on a PERMANOVA test.

962



963

964 **Figure 1.**



965 **Figure 2.**

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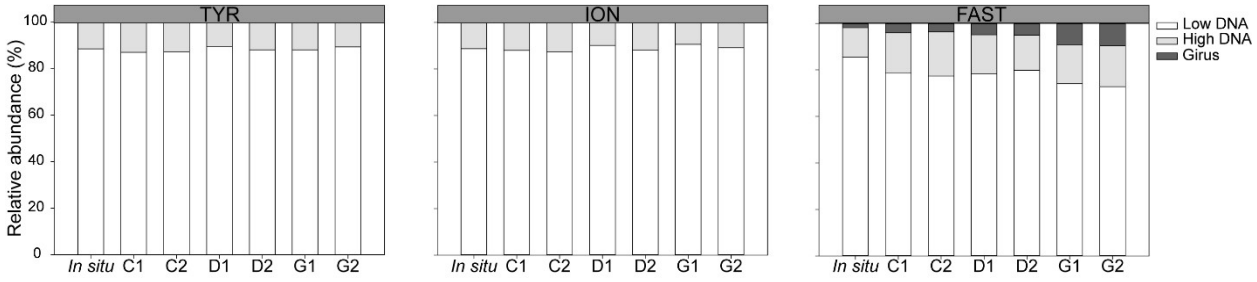

968

969 **Figure 3.**

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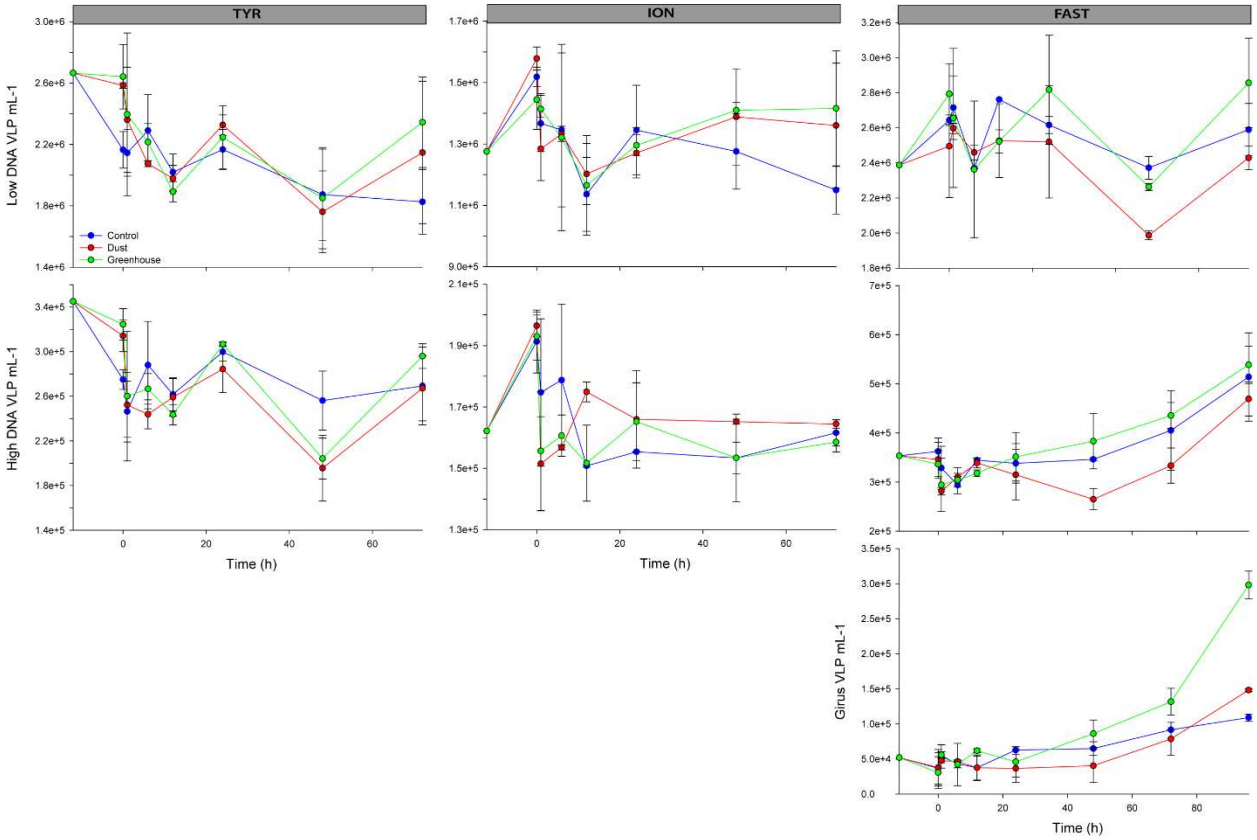
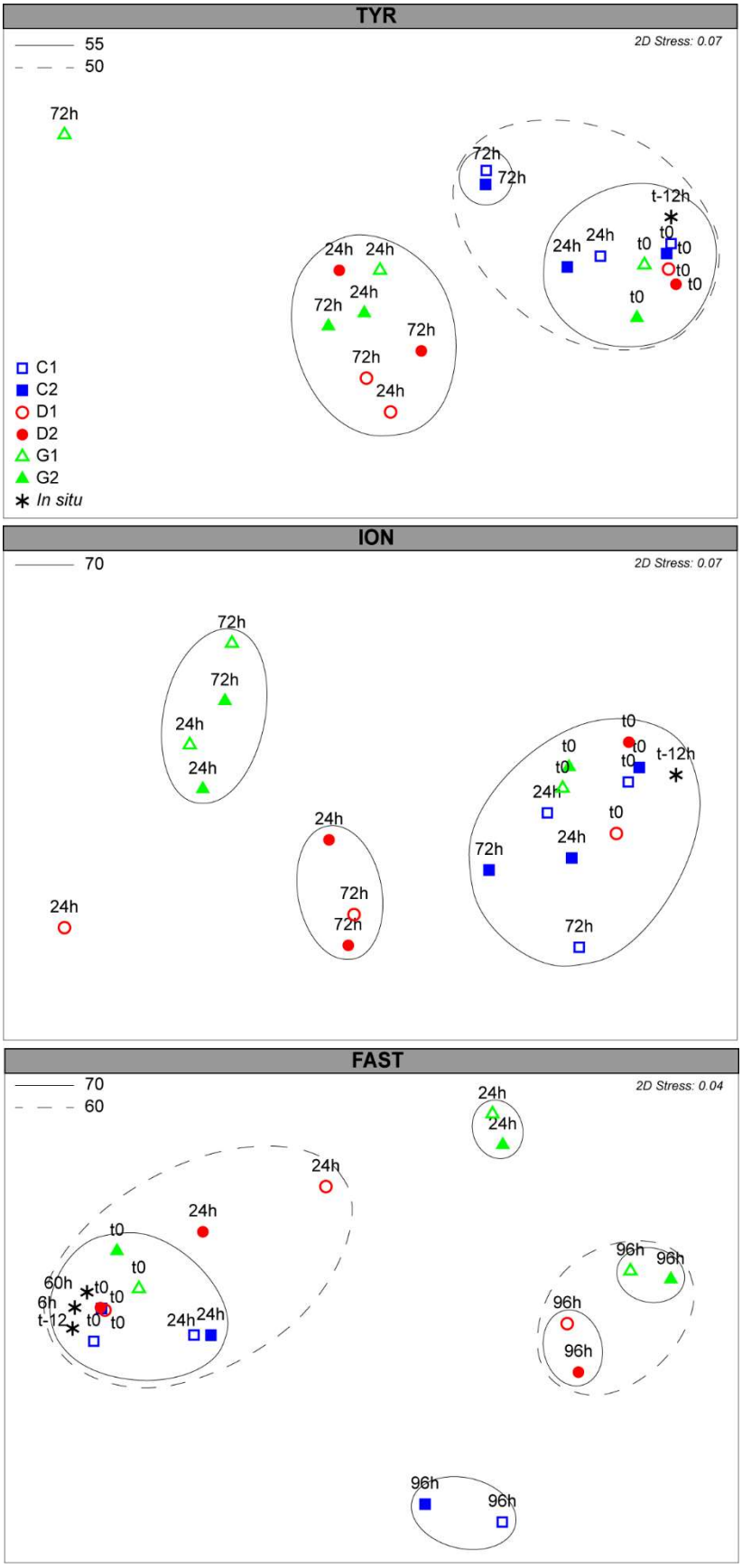


971

972 **Figure 4.**


TYR
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72h
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C1
C2
D1
D2
G1
G2
In situ
ION
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2D Stress: 0.07
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72h
24h
t0
t0
t0
t0
t0
t-12h
24h
t0
24h
72h
72h
FAST
70
60
2D Stress: 0.04
24h
24h
24h
24h
t0
t0
60h
6h
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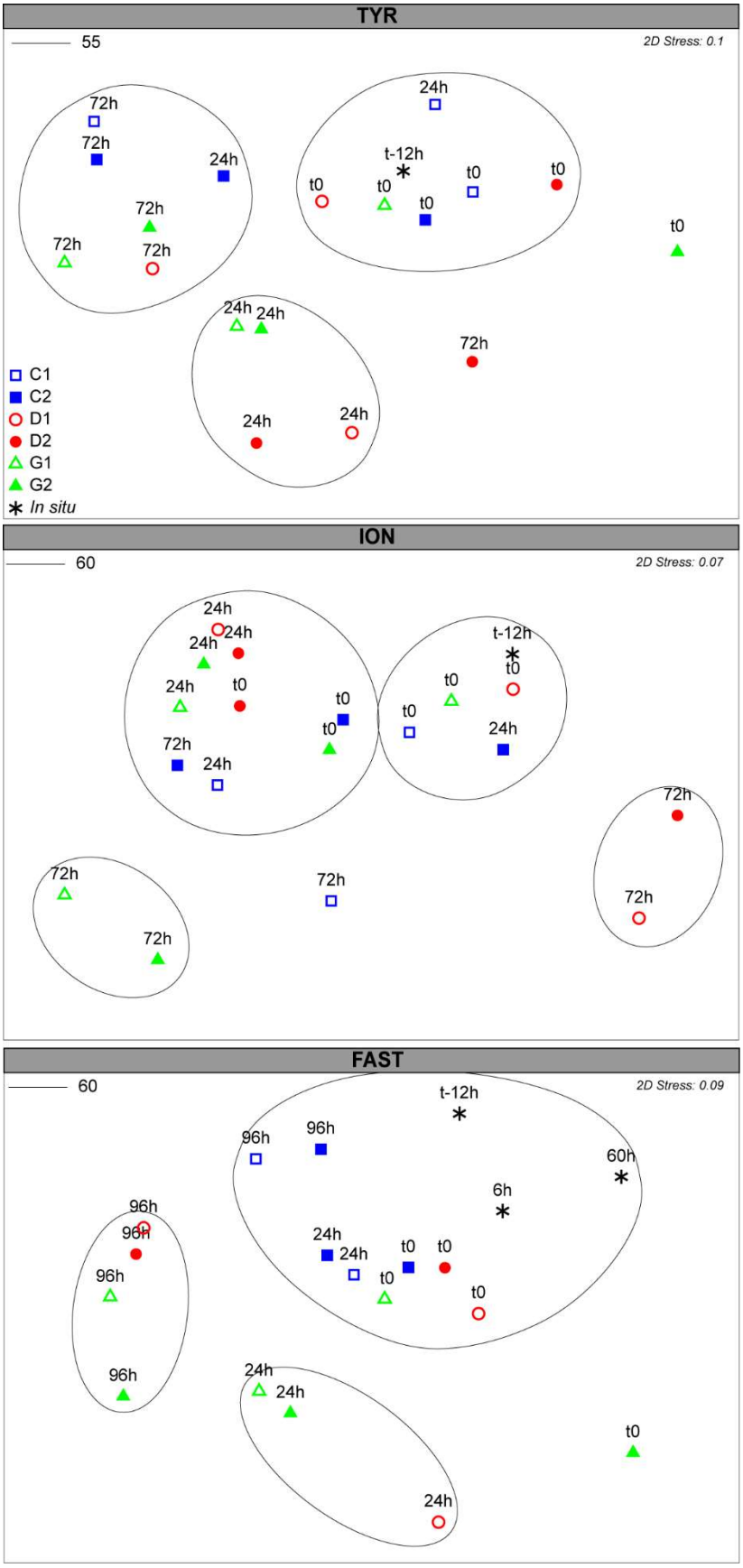
96h

Figure 5.


TYR
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2D Stress: 0.1
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In situ
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2D Stress: 0.07
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72h
72h
72h
72h
FAST
60
2D Stress: 0.09
t-12h
96h
96h
60h
6h
96h
96h
96h
96h
24h
24h
t0
t0
t0
t0
24h
24h
24h
t0

Figure 6.

977